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ECOLOGICAL ENERGETICS OF THE KESTREL: FIELD ESTIMATES OF ENERGY INTAKE THROUGHOUT THE YEAR

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1. INTRODUCTION

Avian reproductive cycles are adapted to seasonal variations in their environment, such that energy demanding processes as reproduction and moult coincide with high food abundance and low thermoregulatory costs. Resource availability in particular has been considered the key element in the evolution of specific temporal programmes, such as the separation of reproduction and moult (Kendeigh 1949, Lack 1968, Perrins 1970, Murton & Westwood 1977). Annual maxima in food availability may allow the extraction of more energy from the environment to cover the increased demand, or alternatively reduce the cost of foraging and maintenance, and hence allow a reallocation of energy. Theoretically, we should expect increased daily energy intake during reproduction and moult under the first hypothesis, and relatively constant intake rates under the second hypothesis.

Adaptive variations in intake rates are well documented for conditions of captivity. Caged birds raise their energy intake in periods of increased demand, such as during moult (*e.g.* King 1980, Thompson & Boag 1976). Also, energy intake in captivity is known to be raised at low ambient temperatures (*e.g.* Kendeigh 1949, Owen 1970, Gessaman 1972, Hamilton 1985). However, metabolism in the absence of moult and cold stress in captivity is lower than in free existence. Therefore the extra costs of moult in nature may be covered by the reduction of thermoregulatory costs in summer, and the same arguments may apply to reproductive costs. This reallocation hypothesis was implicit in Kendeigh's (1972) reconstruction of the House Sparrow's annual energy budget, derived from captivity data. Estimates of intake rates obtained in the field rather than captivity are therefore necessary for an evaluation of the hypotheses.

Variations in Daily Metabolizable Energy (M) are theoretically subject to two constraints. The minimum amount of energy required is equal to the Basal Metabolic Rate (BMR) plus the expenditures in procuring and digesting the food. Since the Heat Increment of Feeding (HIF) amounts to values between 6 and 45% of the energy metabolized, depending on the quality of the food (Ricklefs 1974), the absolute lower limit of M should be somewhere near 1.5 BMR, but more likely 2 BMR if the foraging costs are taken into account. An upper limit to daily energy intake is presumably set by the digestive system (Kleiber 1933, 1961). The allometric relationship for maximal intake rates established by Kirkwood (1983) suggests that this limit constrains intake rates to roughly 4-5 BMR in birds. Thus, natural intake rates may be expected to potentially vary two- to threefold. This leaves ample space for M variations, in addition to reallocation, to contribute to the seasonal programming of reproduction and moult.

Little is known about seasonal variability in natural M in birds. Most reconstructions have made use of extrapolations from energy expenditure and existence metabolism measured in captivity. Accurate measurements of intake

rates in nature usually cover only part of the annual cycle (*e.g.* Hintz & Dyer 1970, Wakeley 1978, Ebbinge *et al.* 1975, Ashkenazie & Safriel 1979, Drent *et al.* 1979, Koplin *et al.* 1980, Wijnandts 1984) and are therefore insufficient to address the role of M variations in enabling reproduction and moult. Furthermore, increases in energy intake may anticipate phases of increased demand, such as in geese and waders during premigratory fattening (Drent *et al.* 1979, Pienkowski 1982, Puttick 1980). Such complications again make clear that a complete year-round analysis of natural intake rates is required.

In a seven year study on the Kestrel *Falco tinnunculus* (see Rijnsdorp *et al.* 1981, Daan *et al.* 1986, Masman *et al.* 1986) we have observed food intake of individual birds for virtually complete days in their natural habitat and in all phases of their annual cycle. From these field observations, in combination with laboratory measurements of prey composition and assimilation, a reconstruction of the variations in M through the annual cycle was made for both sexes. We report here on these seasonal variations and on the dependence of M on weather conditions and behaviour. Elsewhere the associated changes in the use of time for different behaviours will be addressed (Masman *et al.* 1986). In a subsequent article we shall reconstruct how the daily energy available is allocated to different activities and discuss the energetic basis of seasonal organization.

2. METHODS

Estimations of Daily Metabolic Energy (M) were based on complete days of observation of individual Kestrels in the Lauwersmeer area (53 20'N, 6 12'E), and derived for each Kestrel day by means of the following equation:

$$M = \frac{\alpha}{f} \cdot \sum_{i=1}^{n} (k_i.l_i.q_i) \text{ kJ/day} \qquad (1)$$

where n = number of meals per day; k_i = mass estimation of prey number i(g); l_i = energy content of prey type i (kJ/g); q_i = assimilation quotient for this prey type; α = length of the activity time of Kestrels at this date (h); f = length of observation time, *i.e.* the time the bird was actually seen (h).

2.1. BEHAVIOURAL OBSERVATIONS (f)

Individual birds were tracked from dawn to dusk, as described by Masman *et al.* (1986). Among 653 behavioural protocols, we selected those 375 which obeyed the following criteria: 1) length of the protocol time was more than 75% of the active day (α = civil daylength – 0.71 h, as established by Masman *et al.* 1986); and 2) the bird was actually observed for more than 75% of the protocol time (f, h). All prey eaten were scored, when possible specifying species and meal duration in sec. The meals from the daily behavioural protocols were put on file and specified for prey type, part eaten and the time of the day the meal was taken. These data were analysed with the university Cyber computer using a number of special programs and available SPSS routines.

2.2. PREY MASS ESTIMATION (k_i)

During the 375 observation days, 1944 prey were observed to be eaten. For 43 of these (2.2%) prey species and body mass are known since they had been cached by the Kestrel and subsequently weighed by us and replaced. For 879 mammalian prey (45.2%) we recorded the meal duration (t, sec) and used a mass estimation based on the equation:

$$k_i = 0.64.t^{0.59} \text{ g} \qquad (2)$$

This equation was derived by least-squares fitting from 41 instances in which a Kestrel had been observed to cache a prey and subsequently retrieve and eat it, and where both prey mass and meal duration were recorded (Fig. 1).

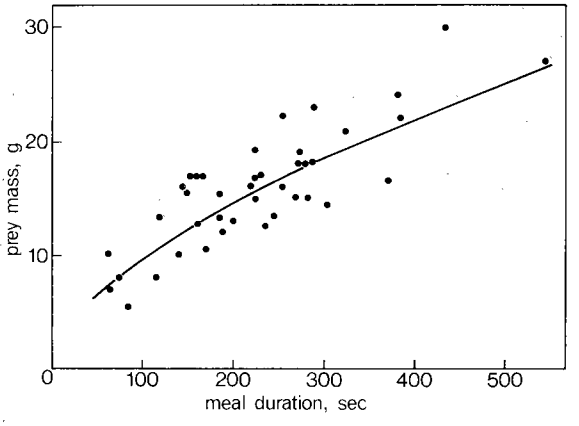

Fig. 1. Prey mass (g) as a function of observed meal duration (sec). Each dot represents one small mammal cached, retrieved and eaten by a Kestrel, for which both prey mass and eating time were recorded. By least-squares fitting the equation: $y = 0.64\ X^{0.59}$ ($n = 41$; $r = 0.833$; $p < 0.001$) was derived.

A further 1022 meals (52.6%) concerned prey known to be either small mammals or birds, occasionally specified as common vole *Microtus arvalis*, common shrew *Sorex araneus*, small songbird or juvenile wader. Since common voles dominate the Kestrels menu in our study area it is of special importance to correctly estimate the mass of a prey of this species, taking prey size selection into account. Four sources of data yielded mean body mass estimations for common voles in the area: voles trapped in regular two-monthly break-neck trap censuses (n = 1100), voles cached by Kestrels in the field and weighed by us (n = 71), voles for which Kestrel meal durations were recorded (n = 879) and

voles delivered by Kestrel parents to their nestlings and weighed by us (n = 239). The estimates are presented in Table 3. Common shrews were less variable in body mass than voles and a figure of 9.8 g could be used throughout. For mammals of unknown species estimates were derived by weighing vole and shrew mass by their frequency of occurrence in the diet in the different phases of the annual cycle (Table 3). Birds in the diet were more variable in mass than mammals and are therefore more difficult to estimate correctly. They had, however, only a minor share in the total food (Table 1), and the intake figures are therefore relatively insensitive to bird mass estimates.

In some cases it was necessary to apply a correction for prey eaten only partially. We further included a correction for uncertain meals. Uncertain meals occurred after a strike was observed in high vegetation and the Kestrel flew up again without prey after more than 3 min, so that prey capture and eating might or might not have taken place. Such uncertain meals followed 383 out of 6354 strikes (6.0%). In such cases we added one prey of average mass multiplied with the monthly strike success rate (Masman *et al.* 1986), to account for potentially missed meals. Kestrel prey are usually eaten only partially: from voles the stomach and small intestines are generally rejected, except by females nursing their broods which frequently swallow these items themselves. The legs and wings of songbirds usually remain at the feeding site. To account for this, estimated prey mass was multiplied by 0.73 for mammalian prey to obtain k_i. This factor was derived from determinations of the mass ratio intenstine/body (0.27 ± sd 0.05; n = 100) of common voles. For avian prey, estimated prey mass was multiplied by 0.70, based on dry mass determinations for a fresh sample of accidentally drowned juvenile Avocets (m = 5.47 ± sd 1.66 g; n = 28; dry mass of intestines, wings and legs: m = 1.30 ± 0.43 g and skin: m = 0.82 ± 0.30 g), under the assumption that half of the skin is consumed.

2.3. PREY COMPOSITION AND ENERGY CONTENT OF PREY TYPE (l_i)

Prey composition with respect to water, fat and protein contents was established on samples of prey obtained in the field. Common voles and common shrews were obtained during the two-monthly break-neck trap censuses. For every period a representative sample was selected by taking 4 voles for each of 5 categories of body mass (5–10; 11–15; 16–20; 21–25 and 26–30 g). For common shrews this was done only once. Water, fat and protein contents were determined for body and intestinal tract separately. Water content was determined by drying for 48 h at 100 °C. The decrease of the dry mass after fat extraction in petroleum ether for 14 h yielded the fat content. The decrease in mass induced by ashing this dry fat-free residue for 4 h at 400 °C, was interpreted as the protein content, assuming minimal carbohydrates present in the samples (Ricklefs 1974).

Bird prey items were obtained from Kestrel nest-boxes during the nestling phase. In weekly nest-box inspections and during continuous observations of Kestrel broods, fresh avian prey items were removed and replaced by laboratory mice. The water content of these birds were determined on the complete items in the same way as on mammalian prey items.

Dried samples of the different prey types were ground in a ultra- centrifugal mill (Retsch) and the caloric values of the samples were determined using a adiabatic bomb calorimeter (Gallenkamp). Duplo or triplo determinations of each sample were carried out and the calorimeter was regularly calibrated with benzoic acid.

2.4. ASSIMILATION QUOTIENT OF PREY TYPE (q_i)

A determination of the metabolic energy (M), retained from the gross Daily Energy Intake (I), was carried out six times (in January, March, May, July, September and November) with two Kestrels (♂, ♀) which had been kept in captivity for several months before the experiments started, and once for two wild males immediately after capturing. The birds were allowed to acclimate to the experimental conditions and to the different diets for three days before the actual measurements were carried out. Each experimental trial lasted three days. The experiments were done in outdoor cages. The birds were trained by falconry methods to sit quiet, tethered on a perch above a glass-plate of 75 x 80 cm, surrounded by vertical plastic sheets to prevent spilling of food and droppings. Food was always given 1 to 2 h before sunset. At the same time the plates with the spilled food, pellets and droppings were collected. Pellets and wasted food were carefully separated from the droppings and all components were dried for 48 h at 100 °C. The Kestrels were weighed daily just before offering the food. In this way records of food intake, Kestrel body mass and weight of the excreta produced were collected for 24 h periods. The energetic content of food (I) and excreta (W) were determined as described for the energetic content of the different prey types. The assimilation quotient (Q) was then calculated over 72 h periods as:

$$Q = \frac{I - W}{I} \qquad (3)$$

During each experiment the assimilation quotient of a common vole diet was established. The food consisted of voles trapped at that time of year. Voles of different body mass categories were offered in a ratio representative for the common vole population in the study area for that time of year as established in the trap census.

Common shrews and birds are primarily taken in summer by the Kestrels in our study area. For this reason the assimilation quotients of common shrew and bird diets were determined only once in July/August.

3. RESULTS

3.1. DIET, PREY SELECTION AND PREY MASS

For the Kestrels in our study area small mammals are the main food source (Table 1). During the behavioural observations analysed here, only 37.3% of all prey items eaten could be identified at the species level. The relative occurrence of the different species, however, is consistent with analyses of Kestrel pellets obtained from our study area. From these it emerges that common voles dominate in the menu throughout the year. During winter (October- March) almost all identified prey items were small mammals

Table 1. Overall diet composition as established from the Kestrel behaviour protocols. Number of prey observed in Kestrels of all phases and sexes combined

Species or species group	Number observed (fraction of total)
Microtus arvalis	573 (29.5%)
Sorex araneus	41 (2.1%)
Unidentified vole or shrew	1208 (62.1%)
Mamals	1822 (93.7%)
Sturnus vulgaris	17 (0.9%)
Small songbirds	13 (0.7%)
Juvenile wader	80 (4.1%)
Unidentified bird	12 (0.6%)
Birds	122 (6.3%)

(95% common voles and 2% common shrews). In summer (April-September) the relative frequencies in the diet of the common shrew (6%), songbirds (2%), and juvenile waders (1%) increased, but it is obvious that also in summer the feeding ecology of the Kestrel in our study area is organized around the common vole as the major food source (Masman *et al.* 1986).

The dominance of the common vole in the Kestrels menu makes it of special importance to apply correct estimates for the mass actually eaten of a prey item of this species. The available vole mass estimates were obtained from four sources: 1) the mass of cached voles, determined by observers after finding the cache, 2) the Kestrel meal durations, 3) the mass of the voles delivered as determined during observations with weighing platforms in the nest-boxes, and 4) the voles collected in the break-neck trap censuses.

A prey capture is always followed by one of three actions. The prey can be eaten immediately after capture, it can be delivered to the dependents, and it can be cached. The frequency distributions of the vole mass categories in these three sets of data are shown for males in April and May in Figs.2A, B and C respectively. From the behavioural protocols it is known that after 60.7% of all (537) prey captures in these months a prey delivery to the female or the nestlings ensues. In 24.0% of all cases the vole is eaten immediately. The final category, voles cached, comprises 15.3%. By multiplying the frequency distributions of Figs. 2A-C with these proportions the body mass frequency distribution for voles caught by male Kestrels was constructed (Fig. 2D). This distribution can be compared with the distribution of body mass of voles trapped in April and May (Fig. 2E).

In the season when the male is foraging for himself, his female and his nestlings (April-July)

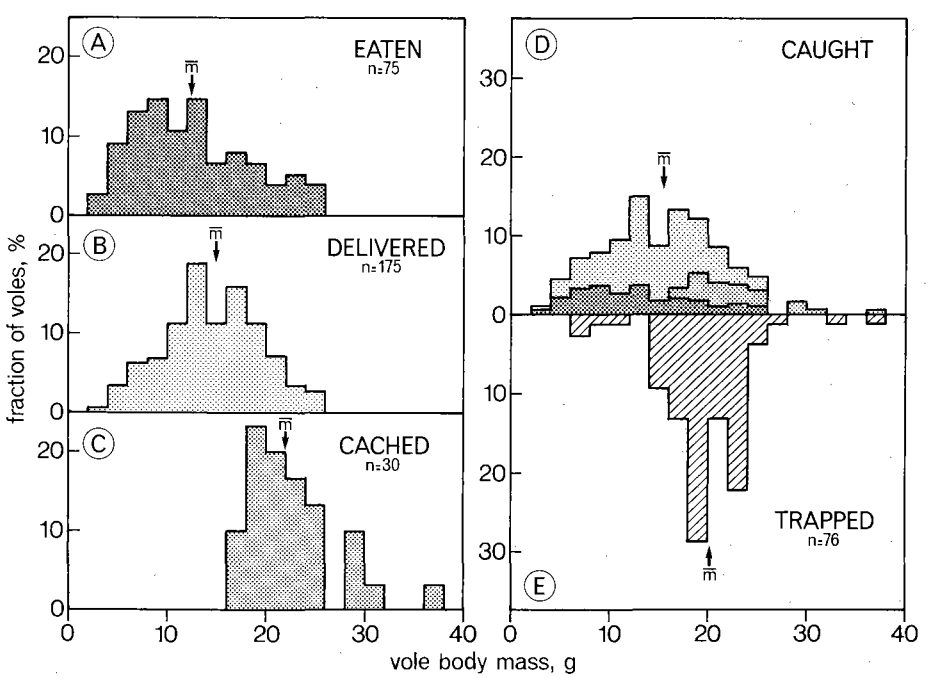

Fig. 2. Left panel: Frequency distribution of the body mass of A: voles eaten immediately after capture, B: voles delivered to the dependents and C: voles catched, for males provisioning their females and/or nestlings in April and May. Right panel: D: Reconstruction (as explained in text) of the relative frequencies as a fraction of all voles caught by the male, E: frequency distribution of the body mass of voles trapped in this period. Mean mass of each population ($\bar{m}$) is indicated.

Table 2. Mean mass (g) of voles eaten, delivered to dependents or cached by the Kestrels and of voles trapped in break-neck traps in different episodes of the year in our study area. The difference between the different categories of voles was tested by Mann-Whitney U-test. Differences between the size frequency distribution of voles trapped and the distribution of voles caught by Kestrels (constructed as explained in the text) were tested by χ^2-test

	♂♂ in April/May	♂♂ in June/July	♂♂ and ♀♀ in August/Sept.	♂♂ and ♀♀ in Oct.–March
	mean ± sd (n)	mean ± sd (n)	mean ± sd (n)	mean ± sd (n)
Voles eaten	12.4 ± 6.0 (75)	11.5 ± 4.1 (76)	11.8 ± 4.9 (72)	15.6 ± 4.4 (210)
delivered	14.8 ± 4.9 (179)	16.1 ± 7.4 (134)	—	—
cached	22.0 ± 5.0 (31)	25.0 ± 4.1 (9)	17.0 (1)	16.2 ± 3.5 (20)
U eaten-delivered	$p < 0.002$	$p < 0.002$	—	—
U eaten-cached	$p < 0.002$	$p < 0.002$	—	ns
U delivered-cached	$p < 0.002$	$p < 0.002$	—	—
Voles caught	15.3 ± 5.9	16.2 ± 7.4	12.8 ± 5.1	15.6 ± 4.1
trapped	20.2 ± 4.9 (38)	17.5 ± 5.6 (127)	15.9 ± 3.7 (474)	16.3 ± 1.9 (359)
χ^2 caught-trapped	$p < 0.002$	$p < 0.05$	$p < 0.002$	ns

the voles eaten by the male have a significantly smaller mean body mass than the voles delivered to his dependents (Table 2). The voles cached by the male have a larger mean body mass than the voles delivered, a difference which is statistically significant for the period April/May (Table 2). In winter the mean body mass of voles eaten and of voles cached are statistically not distinguishable (Table 2). The comparison between vole sizes caught by Kestrels and voles trapped also reveals a difference in summer and not in winter. In summer the voles caught by the Kestrel are on average significantly smaller than the voles trapped. In winter when the vole population is non-reproductive and homogeneous in size, mean body mass for voles caught by the Kestrel and for voles trapped are again not distinguishable (Table 2).

Whether prey size selection during foraging occurs in the Kestrel is not clear. We do not in fact know whether the Kestrels sample or our trap sample is more closely representative for the voles present in the study area. Most probably both samples are biased, but differently. However, it is clear that the decisions, made by a male Kestrel in the reproductive season after a vole has been caught, are at least partly dependent on the body mass of the prey item. There seems to be a preference for caching the heavier voles and for immediate consumption of the smaller ones. Caching is an activity which takes time and energy. The prey has to be hidden and the caching spot has to be inspected, the prey has to be transported to the caching spot and the Kestrel has to fly back to this spot in order to retrieve it. Investing time and energy in caching a smaller prey item is probably less profitable than in a larger prey item, assuming that the investment of time and energy and the chance of losing a cached prey to other animals are nearly independent of prey size.

The preference for delivering a special prey mass category to the nest is less obvious. Probably this decision does not only take circumstances in the male's energy balance into account, but also the energy demand of the female and the nestlings. The time elapsed since the last delivery is probably more important for the decision to deliver a prey than the mass of the prey item caught. During winter the mean mass of cached prey is not different from that of voles eaten immediately, due to the homogeneity of the vole population which reduces opportunities for selection.

The selective treatment of prey by male Kestrels made it necessary to derive, for those cases in which no meal duration was measured, prey mass estimates, differentiated for the sexes and for the different phases of the annual cycle. For each category the mean vole and small mammal body mass estimated from measured meal durations is presented in Table 3. For prey items identified as common shrew one estimate was used throughout (mean mass = 9.8 ± sd 3.6 g; n = 21), also based on meal duration scores. The mean body mass of juvenile waders was derived from prey items brought to the nest (mean mass = 26.2 ± sd 17.1 g; n = 16). For other bird prey

Table 3. Prey mass (g) estimation, mean ± sd (n), applied when no eating time available, derived from 649 recorded meal durations. (632 voles and 17 unidentified small mammals). Note: 1) included are 29 prey eaten by a bigamous male with two females in different phases

Phase	October-March ♂♂, ♀♀	April/May ♂♂	♀♀	June/July ♂♂	♀♀	August/Sept. ♂♂, ♀♀
1 Winter unpaired	14.4 ± 3.9 (107)	—	—	—	—	12.1 ± 2.7 (6)
2 Winter paired	16.7 ± 4.6 (105)	16.8 ± 6.0 (4)	—	—	—	—
3 Courtship feeding	—	18.7 ± 2.1 (7)	17.2 ± 5.4 (18)	—	—	—
4 Egg laying	—	16.4 ± 5.2 (12)	15.9 ± 4.8 (45)	—	—	—
5 Incubation	—	12.5 ± 6.1 (14)	13.4 ± 4.6 (129)	15.0 ± 3.6 (5)	—	—
6 Nestlings ≤ 10 d	—	12.5 ± 5.7 (8)	15.4 ± 7.5 (4)	10.7 ± 4.3 (23)	—	—
7 Nestlings > 10 d	—	12.9 ± 6.8 (7)	—	11.5 ± 3.9 (43)	13.5 ± 55. (11)	—
8 Dependent fledglings	—	—	—	12.1 ± 4.9 (5)	—	11.5 ± 3.4 (7)
9 Moult	—	—	—	—	—	11.7 ± 5.3 (60)
All phases	15.5 ± 4.4 (212)	12.9 ± 6.1 (81)[1]	14.4 ± 5.0 (196)	11.5 ± 4.1 (76)	13.5 ± 5.5 (11)	11.7 ± 4.9 (73)

we had to work with mass estimates from literature (*Sturnus vulgaris* : 70 g ; small songbirds: 25 g). For unidentified bird prey we used the estimate of 33 g (*i.e.* the mean of all bird prey categories). While these latter estimates are admittedly inaccurate, the final daily intake rates are hardly sensitive to these values since these bird species occur so infrequently in the diet.

3.2. PREY COMPOSITION

Water, fat and protein contents of the common voles analysed varied with season (Table 4). In summer water contents were higher than in winter. This may partly be due to the high water content of juvenile voles (mean mass: 9.0 ± sd 4.0 g; water content: 72.8 ± 1.4%; n = 11) and gravid females (mean mass: 24.5 ± 4.0 g; water content: 74.2 ± 2.1%; n = 8), relative to that of the subadult winter voles, but an increase in water content was found for all body mass categories.

The fat content of dry body mass was lower in summer, while the protein content was higher (Table 4). The ash fraction was higher in winter than in summer, probably due to a heavier fur coat of the winter voles and the relatively less developed bones of the juvenile summer voles. The energy content per g dry matter (mean:

Table 4. Seasonal variation in prey composition, mean ± sd (n). Notes: 1) mean for May-September; 2) mean for October-March; ANOVA test for summer-winter differences: * $p < 0.0005$, n.s. = $p > 0.05$

Species	Period	Water	Fat	Protein	Ash	Energy
Microtus arvalis	January	66.3 ± 0.9 (8)	14.1 ± 2.7 (8)	70.8 ± 3.4 (6)	15.4 ± 1.1 (6)	21.6 ± 0.2 (7)
	March	67.5 ± 1.7 (12)	14.4 ± 3.0 (12)	71.6 ± 3.7 (10)	14.4 ± 1.1 (10)	21.4 ± 0.2 (12)
	May	72.2 ± 2.2 (21)	10.2 ± 3.9 (20)	76.2 ± 3.2 (15)	13.7 ± 1.8 (15)	21.3 ± 0.1 (20)
	July	72.1 ± 1.5 (20)	10.1 ± 4.1 (20)	76.2 ± 4.2 (15)	12.4 ± 1.5 (15)	21.6 ± 0.2 (14)
	September	71.5 ± 0.7 (8)	11.1 ± 1.0 (8)	74.2 ± 1.8 (6)	13.8 ± 1.2 (6)	21.1 ± 0.2 (4)
	November	68.3 ± 1.0 (8)	12.9 ± 2.5 (8)	71.9 ± 2.2 (6)	14.1 ± 0.6 (6)	21.6 ± 0.4 (5)
	summer[1])	72.0 ± 1.7 (49)	10.3 ± 3.7 (48)	75.8 ± 3.5 (36)	13.2 ± 1.7 (36)	21.4 ± 0.6 (38)
	winter[2])	67.7 ± 2.2 (28)*	13.9 ± 2.8 (28)*	71.4 ± 3.2 (22)*	14.6 ± 1.1 (22)*	21.5 ± 0.5 (33) ns
Sorex araneus	summer	69.3 ± 0.5 (4)	9.3 ± 0.5 (4)	80.5 ± 1.6 (2)	10.6 ± 0.9 (2)	21.6 ± 0.4 (5)
Vanellus vanellus juv.	summer	75.4 (1)	—	—	—	24.1 ± 0.1 (2)
Limosa limosa juv.	summer	73.2 (1)	—	—	—	21.3 ± 0.7 (4)
Haematopus ostralegus juv.	summer	72.1 (1)	—	—	—	22.7 ± 0.1 (2)
Birds (mean)	summer	73.6 ± 1.7 (3) % fresh mass	— % dry mass	— % dry mass	— % dry mass	22.3 ± 1.3 (8) kJ/g dry mass

21.4 ± sd 0.6 kJ/g; n = 62) did not show significant seasonal variations, which confirms Gorecki's (1967) findings.

Analyses of the common shrews and birds were only carried out in summer because in winter these prey types are virtually absent from the diet (Table 1). The composition of common shrews was nearly identical with that of the summer voles. The water content as well as the energy content of dry matter of birds tended to be higher than that of the small mammals.

3.3. ASSIMILATION QUOTIENT (q_i)

Energy retention from a common vole diet was highest in summer (Table 5). The energy not assimilated is measured as the total energy content of the faeces and of the pellets. Relative to gross energy intake the total energy content of the pellets in winter was significantly higher than that in summer (Student t test; $p < 0.005$). One of the explanations might be that digestibility increases when the thickness of the fur coat of the voles decreases. Heavier fur is probably responsible for higher ash fractions in common voles in winter and has been described for *Microtus pennsylvanicus* under artificial long days (Dark & Zucker 1983).

Table 5. Seasonal variation in assimilation quotient of a common vole diet and the assimilation quotient of a common shrew, a lab mouse and a bird diet, (mean ± sd, n); notes: 1) determined on two male Kestrels, caught one week before the experiment; 2) mean for summer trials (May-September); 3) mean for winter trials (October-March). p-values indicate significance of differences between consecutive monthly trials and between summer and winter (ANOVA). Asterisks indicate significant difference to previous value (* $p < 0.05$; ** $p < 0.0005$)

Diet	Period	Assimilation quotient × 100
Microtus arvalis	January	66.2 ± 1.7 (6)
	March	66.8 ± 1.2 (4)
	May	69.8 ± 2.7 (3)*
	July	72.4 ± 2.6 (12)
	September	67.8 ± 1.4 (5)**
	November	67.6 ± 2.0 (3)
	December[1])	62.2 ± 9.2 (4)
	summer[2])	70.4 ± 3.0 (20)
	winter[3])	66.7 ± 1.6 (13)**
Sorex araneus	summer	64.8 ± 0.5 (5)
Birds	summer	75.2 ± 1.4 (3)
Laboratory mouse	summer	78.4 ± 1.3 (11)

In some herbivorous bird species it has been demonstrated that the assimilation quotient for a standard diet was different for birds kept in captivity and birds freshly caught from the wild, presumably related to functional changes in the intestinal tract (Moss 1977). There is no evidence that this phenomenon also occurs in carnivorous birds. The assimilation quotient for a common vole diet, determined on two freshly caught Kestrels in December was not different from that determined on permanently captive birds in winter (Table 5).

The assimilation quotient for a common shrew diet was statistically not distinguishable from that for a common vole diet in summer (ANOVA test, $p < 0.001$).

In the calculation of energy intake (equation 1) the estimate of the ingested small mammal dry biomass (k_i) was multiplied by the energetic equivalent (l_i) of 21.4 kJ/g throughout (Table 4). The resulting figure for the gross energy intake was multiplied again by the assimilation quotient (q_i) of 0.67 for the winter meals, by 0.70 for the summer vole-meals and by 0.65 for the summer shrew-meals (Table 5), to obtain metabolizable energy intake (M).

For ingested avian prey items we used the assimilation quotient determined on a mixed diet consisting of juvenile waders (*Vanellus vanellus*, *Limosa limosa* and *Haematopus ostralegus*). The assimilation quotients determined for mammal and birds are in good agreement with figures from the literature for energy retention from mammal and bird diets by the Kestrel (Kirkwood 1981) and other raptors and owls (Wijnandts 1984, Tollan 1986).

3.4. VARIATION OF ENERGY INTAKE WITH TIME OF DAY

Energy is needed throughout the 24 h cycle. In the Kestrel food intake is restricted to the daylight period and meals are not evenly distributed over the day. Rijnsdorp *et al.* (1981) observed that meal frequency increased in the last hour before sunset. In this study the data originally used by Rijnsdorp *et al.* (1981) were substantially expanded and meal frequencies were converted to energy intake rates in order to take meal size variation into account (Fig. 3).

Data for both sexes in the non-reproductive season were combined. The analyses of data ob-

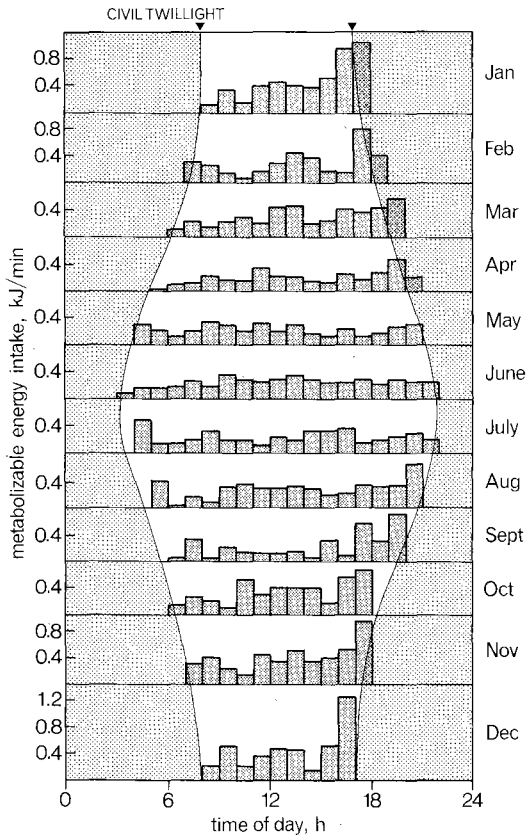

Fig. 3. Variation of metabolizable energy intake (kJ/min) with time of day. Data for all complete observation days combined per month, except those for females during courtship feeding, egg-laying, incubation or brooding nestlings < 10 days (phases 3, 4, 5 and 6). Bars indicate mean energy intake in each hour interval (total observed energy intake was divided by total observation time). Shaded area indicates nocturnal rest.

tained in the reproductive season were restricted to birds providing their own food, thus excluding females during phases 3 (courtship), 4 (egg laying), 5 (incubation), and 6 (nestlings ≤ 10 days old). In the non-reproductive season (September-March) energy intake rate increased at the end of the active day (Fig. 3). In contrast energy intake in the reproductive season was constant over the daily active period. The data for females in phases 3, 4, 5, and 6 were analysed separately and show the same pattern as males in the reproductive season. The same annual pattern was described by Rijnsdorp *et al.* (1981) for meal frequencies with the exception of a single male during incubation for whom the data showed a peak in meal frequency at the end of the active period. This phenomenon was used by the authors to advance the hypothesis of a general energy saving policy by the males keeping body mass during flight at the lowest possible level. Our new analysis does not support this hypothesis, since both males and females generally abstain from special evening meals in the summer and the one male treated by Rijnsdorp *et al.* (1981) has proved to be an exception. Another benefit of evening meals suggested by Rijnsdorp *et al.* (1981) concerns the more efficient use of the heat produced in food digestion (HIF). Nocturnal exploitation of heat production by HIF is possibly in winter a more important factor to adjust the daily energy balance than in summer. Ambient temperatures are lower and nights are longer. This in itself makes accumulating extra food towards the end of the day adaptive in creating an overnight energy store in winter. An evening feeding peak has also been demonstrated in other bird species (Schmid 1965, Hintz &Dyer 1970, Murton & Westwood 1977, Zeigler *et al.* 1971).

It is clear that daily fluctuations in energy intake rate make it necessary to estimate the mean daily energy intake from observations covering the complete active period.

3.5. VARIATION OF ENERGY INTAKE BETWEEN DAYS

In Fig. 4 a selection of daily energy intake values of three wintering Kestrels, for which data from several days were available, is shown. While there appear to be interindividual differences in M, all individuals show relatively large day-to-day variations. These variations are much larger than can be explained by errors in the estimates of meal sizes. They are actually due primarily to variations in the number of similar-sized meals per day.

For its energy intake the Kestrel depends on relatively rare events of prey capture and especially during the short winter days bad weather conditions may cause food shortage for one day. There are severe meteorological constraints on flight-hunting (Rijnsdorp *et al.* 1981, Masman *et al.* 1986) and conditions such as rain and high (> 12 m/sec) or low (< 3 m/sec) wind speeds

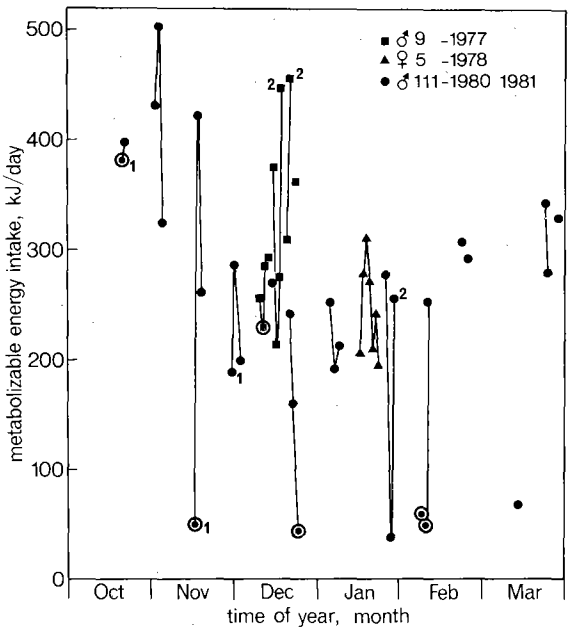

Fig. 4. Day to day variation in metabolizable energy intake in three wintering Kestrels indicated by different symbols (see key). Lines connect consecutive observation days of one individual. Prey retrieved, caught and cached the day before are indicated by 1). Prey cached and not retrieved on the same day are indicated by 2). Days with extreme bad weather conditions: wind speed > 12 m/sec or rain > 5 h/day) are indicated by a circle around the symbol.

contribute to the variation shown in Fig. 4. The food caching and retrieving behaviour as observed in the Kestrel has primary significance in separately optimizing daily times of hunting and of food intake (Rijnsdorp *et al.* 1981, Daan 1981). In addition it may have a function in buffering the effects of days with bad weather conditions. During our observations it was repeatedly recorded that a Kestrel did not retrieve a prey cached during the same observation day, as well as that it retrieved a cached prey early in the active period, which had obviously been cached the day before. In Fig. 4 these prey items cached overnight are indicated. It is clear that on days with inclement weather conditions M may depend heavily on cached prey from the day before. Without such caches, a Kestrel may occasionally face the necessity of mobilizing body reserves. Extremely high intakes in Fig. 4 (M > 400 kJ/day) represent days on which these body reserves were replenished.

3.6. SEASONAL VARIATION OF MEAN DAILY ENERGY INTAKE

Mean daily energy intake varied considerably through the annual cycle (Fig. 5). For both sexes intake rates were highest during the reproductive season and lowest during moult (August-September). During winter mean intake rates for males (275.7 ± se 13.9 kJ/day; n = 64) and females (266.2 ± 20.9 kJ/day; n = 19) were statistically indistinguishable (ANOVA $p < 0.05$). The mean winter M for the sexes combined was 273.5 ± 11.7 kJ/day (n = 83). For males the highest mean intake rate (414.0 ± 38.3 kJ/day; n = 24) was recorded in June. The data set for females was smaller and only permitted the estimation of mean daily energy intake on a two-monthly basis. The highest mean intake rate of females (317.5 ± 70.3 kJ/day; n = 5) was recorded in July/August, an elevation of 16% above the mean winter level.

This annual pattern in intake rates for males and females, and the difference between the

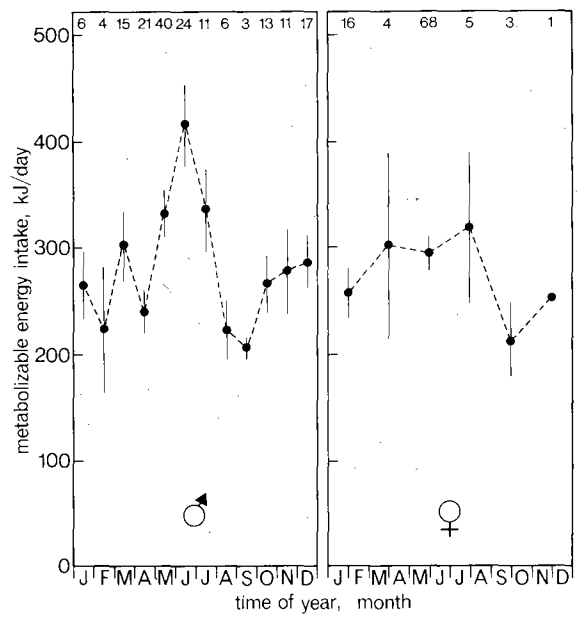

Fig. 5. Monthly mean daily metabolizable energy intake (M) for males (left panel) and bimonthly mean M for females (right panel). Indicated are mean (dots) and standard error of the mean (vertical lines). Days on which more than 25% of the prey captures were uncertain, and on which less than 50% of the prey was actually seen eaten were excluded. Figures on top indicate sample size (nr of days).

Table 6. Mean daily metabolizable energy intake for males and females in the different phases of the annual cycle. Days on which more than 25% of the prey captures were uncertain, or on which less than 50% of the prey was actually seen eaten, were excluded

Phase	Males			Females		
	Mass kg	M kJ/day ± se (nr of days)	Watt/kg$^{0.75}$	Mass kg	M kJ/day ± se (nr of days)	Watt/kg$^{0.75}$
1 wintering unpaired	0.203	285.3 ± 18.9 (24)	10.9	0.244	249.8 ± 21.4 (16)	8.3
2 wintering paired	0.203	243.8 ± 18.0 (43)	9.3	0.244	285.6 ± 49.3 (5)	9.5
3 courtship feeding	0.206	219.6 ± 26.2 (12)	8.3	0.263	251.1 ± 52.6 (7)	7.9
4 egg laying	0.213	266.7 ± 26.7 (19)	9.8	0.305	371.2 ± 32.1 (15)	10.5
5 incubation	0.204	278.5 ± 35.8 (10)	10.6	0.275	309.2 ± 20.6 (33)	9.4
6 nestlings ≤ 10 days	0.188	415.6 ± 42.3 (18)	16.8	0.267	181.5 ± 46.8 (8)	5.6
7 nestlings > 10 days	0.196	390.5 ± 30.0 (26)	15.3	0.235	265.4 ± 45.9 (11)	9.1
8 dependent fledglings	0.173	284.6 ± 89.8 (3)	12.3	0.197	—	—
9 post reproductive moult	0.202	216.9 ± 15.0 (7)	8.3	0.229	197.8 ± 51.7 (2)	6.9

sexes reflects the sequence of reproductive and non-reproductive phases in the annual cycle. Some of the variation between individuals in each month can be accounted for by differences in reproductive stage. In Table 6 the data are rearranged according to the different phases of the annual cycle. In addition, this table provides mean body mass per phase of Kestrels trapped wild in the field (unpublished data from Dijkstra). On the basis of these data, M was expressed per kg 0.75 .

In females the mean intake rate was highest during egg-laying (an elevation of 35% above the winter level), probably associated with the energy needed for the production of the eggs. Mean female body mass is also highest during this phase of the annual cycle. In phase 6 (day 1-10 after egg-hatching) female intake rate dropped to a minimum. From observations at close range we know that females feeding their nestlings eat only small parts of the skin and the intestines of the prey delivered by the male, representing very little energy and presumably serving mainly water suppletion. Correspondingly mean female body mass decreased by 14% from phase 5 till phase 7.

The mean intake rate of the males reached a maximum in the nestling phase (an elevation of 52% above the winter level), associated with the energy needed for the high activity level in this phase (Masman *et al.* 1986). The activity of the males, expressed as the hours per day spent in flight-hunting and directional flight, increases as soon as the male starts delivering prey to its female before egg-laying. This elevation, however, was not observed in the intake rate of the males, which increased substantially only in the nestling phases (Table 6). The discrepancy is reflected in the mean male body mass, which decreases with 14% during reproduction. Intake rates for both sexes reached a minimum during moult (76% of the winter level). The activity level is also minimal in this phase of the annual cycle.

3.7. RELATION OF ENERGY INTAKE AND ACTIVITY

Since the maximum levels of intake and flight activity coincided (males in phase 7) as well as the minimum levels (males and females in phase 9), it is of interest to see whether some of the variability within phases is correlated with differences in activity levels. We therefore analysed the correlation of daily energy intake rates and daily flight hours of male Kestrels tending their nestlings or fledglings (phase 6, 7, 8).

The metabolisable energy intake rate increased significantly with increasing daily time

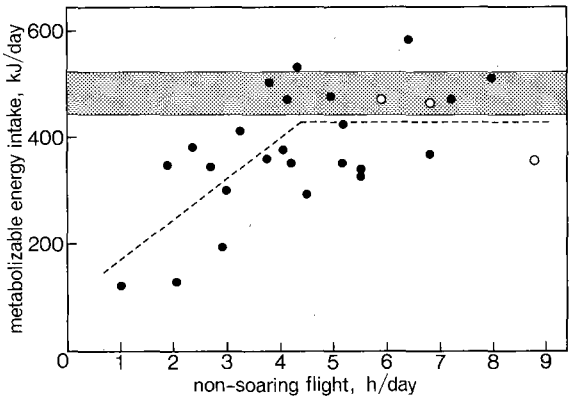

Fig. 6. Daily metabolizable energy intake plotted as a function of time spent flying plus flight-hunting per day, for males in the nestling and fledgling-phases (6, 7 and 8). Each dot represents one complete observation day. Three days on which the food satiation of the nestlings was experimentally reduced (Masman *et al.* 1986), are indicated by open symbols.
Line indicates the linear regression over all days with less than 4.6 h spent in flight and the mean intake rate on days with more than 4.6 h spent in flight. For a Kestrel of 192 g the allometric equation of Kirkwood (1983) predicts a maximal daily metabolizable energy of 522 kJ, the equation of Kleiber (1933) predicts a maximum food capacity of 445 kJ. Grey bar indicates values between those two predicted levels.

spent in flight ($r = 0.56$; $n = 27$; $p < 0.005$). However, the scattering of the data points (Fig. 6) suggests that the positive correlation between intake and activity is due only to the lower values, whereas energy intake tends to level off with increasing time spent in flight. Arbitrarily the data set was therefore divided into two groups: days with flight activity less than the mean level for males tending nestlings (4.6 h/day; Masman *et al* . 1986) and days with flight activity above this mean level. On days with less than 4.6 h flight, daily metabolizable energy intake (M in kJ/day) was linearly correlated with time (F in h) spent flying plus flight-hunting ($M = 96.3 + 76.1$ F; $r = 0.65$; $n = 15$; $p < 0.01$). The slope of this regression line points at an increase in energy intake of 76.1 kJ for each hour spent in flight. The cost of flight in the Kestrel (52 kJ/h,unpublished data) falls within the 95% confidence limits of this slope (23.0-129.2 kJ/h). Thus a tentative interpretation is that on days with flight activity less than 4.6 h a male Kestrel is able to maintain a balance between energy intake and expenditure.

On days with more than 4.6 hours devoted to flight there was no significant relation between the time spent in flight and the energy intake rate ($M = 372.0 + 9.1$ F; $r = 0.1361$; $n = 12$; $p < 0.05$), but energy intake varied around a mean level of 430.0 kJ/day (se = 23.4) . There is no reason to assume that the power consumption during flight decreases with increasing time spent in flight. The data therefore suggest that on days with high activity levels energy intake is usually insufficient to cover energy expenditure, and energy from body reserves has to be mobilized under these circumstances.

4. DISCUSSION

Daily food intake fluctuated considerably in the Kestrel. The species seems to vary in its annual cycle across the range of possible variation in daily metabolizable energy intake (M). Variations in M are related to marked differentiation in the division of labour between the sexes and to differences in time allocation in the various phases of the cycle (Masman *et al.* 1986), as discussed below.

During winter both sexes forage by hunting both from perches and in windhovering flight. In this season Kestrels spend on average 1.5 h flying + flight-hunting. As in April reproduction starts, the female stops foraging for herself and the male provides the female with food. His foraging behaviour shifts, and almost all prey items (94%) are caught from flight-hunting. From 14 days before egg-laying, up to the time the nestlings reach the age of 10 days (62 days) the male forages for himself, his female and his nestlings. In the nestling phase he spends on average 4.6 h flight + flight-hunting per day. During reproduction the increased flight-hunting yield (voles/h) is the main factor enabling the increasing daily amount of food gathered by the male, but also his efforts in terms of time spent flying and flight-hunting increase slightly from spring to summer.

The annual variation in daily metabolizable energy intake described here gives an indication of the role of M variations in enabling reproduction. In spring, as ambient temperature rises, the daily energy needed for thermoregulation will decrease. The daily energy needed for activity by the male increases as soon as he starts

feeding his female. His M does not increase until the eggs hatch. In this first part of reproduction it is probably mainly by reallocation of energy that he is able to expand his efforts; in addition body reserves may be used. In the second part of the breeding season, the M of the male increases significantly (Fig. 6), while mean daily effort (h flying + flight-hunting) is hardly expanded further, so that the energy budget is probably more in balance.

For the female during reproduction the situation is different. Her daily energy expenditure for activity reaches a yearly minimum in the period she is fed by the male (phases 3, 4, 5 and 6). During courtship feeding the reallocated energy from thermoregulation and activity seems to be sufficient for gonadal growth since M remains at the winter level. As soon as she starts laying eggs and accumulating body reserves her M is significantly increased. During incubation M is back to the winter level and reallocated energy again seems sufficient for incubation of the eggs. During the first 10 days after the eggs have hatched her M reaches a minimum while she rapidly loses body weight (Table 6). Her increased activity in the second part of nestling care is partly compensated by an increased M rate.

During post-reproductive moult both sexes have very low activity levels as well as low M rates. The reallocated energy from reduced thermoregulation and activity expenses seems to be sufficient for the production of new feathers.

It is obvious that M is restricted by the food availability. On winter days with severe weather conditions foraging and thereby food availability are restricted (Fig. 4). On the other hand, the estimated energetic equivalent of the total prey mass caught per day for males which provision their broods and fly for more than 4.6 h per day is on average 1572 kJ/day (metabolizable energy), ranging from 834 to 2325 kJ/day. In this situation the available energy is not directly constraining the energy intake, while M seems insufficient to cover the daily energy costs (Fig. 7). Kleiber (1933) suggested originally that there is a general mass-specific maximum food capacity in mammals (Food Capacity = 1533. $kg^{0.75}$ kJ/day). The allometric relationship for maximal daily metabolizable energy intake rates established by Kirkwood (1983) for mammals and birds (Mmax = 1713. $kg^{0.72}$ kJ/day) supports this suggestion. The plateau in M (430.0 kJ/day) reached by males which spent more than 4.6 hours per day in flight is close to the maximum food capacities for a Kestrel of 192 g, predicted by Kleiber (1933) and Kirkwood (1983). This suggests that the M of these males is limited by a physiological constraint. It is quite likely that this constraint on the food processing rate eventually determines the maximal work capacity at which altricial birds are found to operate during parental care (Drent & Daan 1980).

Summarizing, we can say that seasonal variation in mean M in the Kestrel is characterized by a rather stable low winter level of 8.6 (♀♀) – 9.9 ♂♂ Watt/$kg^{0.75}$. The summer intake is not simply a rise to maximum levels but is highly dependent on the activities performed by the birds. Intake dropped far below the winter level

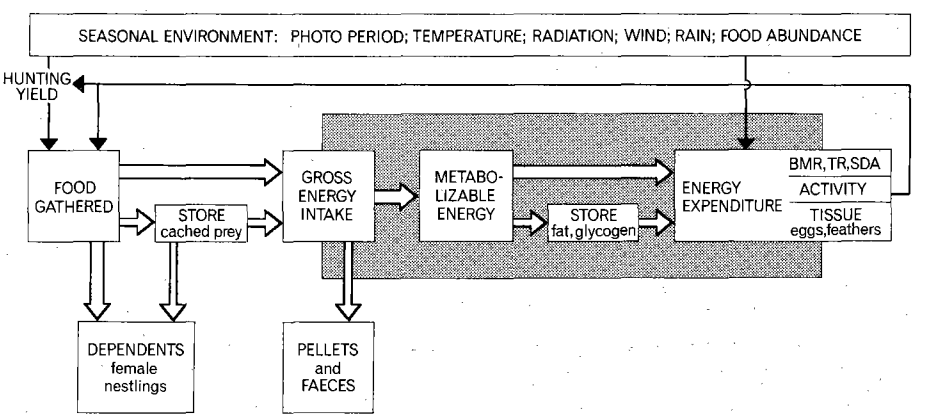

Fig. 7. Diagram of the energy budget of the Kestrel and main pathways for effects of seasonal variations in the environment on energy-intake and -expenditure.

Table 7. Daily metabolizable energy intake estimates for free-living wintering predatory birds. Values for *Falco tinnunculus* are the mean for phases 1 and 2 (table 6)

Species	Sex	Mass kg	M intake (kJ/day)	Watt.kg$^{-0.75}$	Reference
Falco tinnunculus	♂	0.203	258.7	9.9	this study
Falco tinnunculus	♀	0.244	258.3	8.6	this study
Elanus caeruleus	—	0.241	274.8	9.2	Sapsford & Mendelsohn 1984
Asio otus	♂, ♀	0.280	252.3	7.6	Wijnandts 1984
Elanus leucurus	♂, ♀	0.331	474.3	12.6	Koplin *et al.* 1980
Circus cyaneus	♀, juv.	0.500	596.5	11.6	Boedeltje & Zijlstra 1981

during moult in both sexes, just after egg hatching in females and during courtship feeding in males. They rose to annual maxima during parental care in the males and during egg laying in the females.

There are few data available on other raptors in nature – and indeed on any bird species – to compare these results with. Winter food intakes in the wild have been reliably estimated in four species (Table 7), including an accurate tritium-turnover determination of energy intake in Black-shouldered Kites (Sapsford & Mendelsohn 1984). The estimates range from 7.6 to 12.6 Watt/kg$^{0.75}$. They are all below Kestrel peak intakes in the reproductive season, but the variation is considerable. Especially the Long-eared Owl appears to survive on a relatively low daily metabolizable energy intake in winter, as emphasized by Wijnandts (1984). Other published analyses on winter intakes in raptors (Tarboton 1978, Koplin *et al.* 1980, *Falco sparverius*; Sylvén 1982, Raptor Group RUG/RIJP 1982, Beissinger 1983) are less reliable. They do not take into account possible sources of variation which were demonstrated in the Kestrel to strongly affect the obtained estimate of M, such as: variation in intake with time of day (Fig. 3); variation between days, affected by weather conditions (Fig. 4); variation in prey energy content (Table 4, 5); differences between prey sizes available and eaten (Table 2).

Comparison of intake rates in the reproductive season with published data in other raptors is even more difficult due to the large variability between phases of the reproductive cycle. Natural energy intake rates during moult have not been measured in the field and published estimates during egg laying and male parental care are heavily dependent on the assumptions made (Wakeley 1978, Sylvén 1982, Wijnandts 1984). The absolute minimum M in the Kestrel observed in females brooding hatchlings closely corresponds with the drop in M reported by Wijnandts (1984) for the female Long-eared Owl in this phase. This probably reflects a general strategy for birds with marked division of labour between the sexes. It further points to the importance of analysing M in a broader context of seasonal strategies in the use of time and energy including the accumulation and mobilization of body energy stores.

A quantitative analysis of the energy budget of the Kestrel in course of the annual cycle will be presented later. Qualitatively some implications and conclusions can be formulated on the basis of the data analysed here. All available options to enable peaks in energy expenditure: an increased M, the mobilization of body reserves, as well as the reallocation of energy, are used by the Kestrel during reproduction. In general it is clear that energy intake and energy expenditure, in the long run (months, year) have to match. On a shorter term (hours, days, month) these processes can be uncoupled. Food intake can be postponed till the end of the day or till the next day by caching the food. On severe winter days and in episodes of high energy demand from the offspring, a bird has to abandon the option of a sufficient food intake rate. Such restraint is only possible when prior accumulated energy reserves can be mobilized and thus depends on anticipatory behaviour which leads to building up these reserves. Diagramatically the relationships between the seasonal environment, the gross energy intake, and the energy expenditure are displayed in Fig. 7. Seasonal variations in the environment act on both sides of the energy budget. Variations, such as in food abundance and in prevailing weather conditions determine the hunting yield

achieved. On the other hand energy expenditure is partly dependent of these variations such as in temperature and radiation. The choice of hunting mode and the time spent foraging in addition to the hunting yield determine the total amount of food gathered per day. Time allocated to foraging thus plays a crucial role in the energy budget since it determines both the gross energy intake and a large part of the energy expenditure.

The analysis of strategies in time allocation, in daily metabolizable energy intake and thereby in the management of the sources of intrinsic energy are vital in the interpretation of the energy budget of an individual and of the implications for its fitness. In this paper only the daily metabolizable energy intake was addressed. The seasonal variation in time allocation is analysed elsewhere (Masman *et al.* 1986). An interpretation of what the annual variations in M and in time allocation imply for the variations in the daily energy budget requires estimates for the compartments of the daily energy expenditure. We hope to provide these cost factors required in the near future.

5. SUMMARY

1. Daily metabolizable energy intake (M) was estimated on 375 days of dawn to dusk observation of individual free living Kestrels in the different phases of the annual cycle. Prey species, meal frequency and meal duration were obtained from the behavioural protocols. The seasonal variation in energy content and assimilation quotient of the different prey types was established in the laboratory.

2. During winter (October-March) prey were primarily small mammals (95% common vole *Microtus arvalis*, 2% common shrew *Sorex araneus*). In summer (April-September) the diet was still dominated by the common vole (91%) but the relative frequencies of common shrew (6%), songbirds (2%) and juvenile waders (1%) increased (Table 1).

3. Common vole mass estimates were obtained from four sources: 1) cached voles, weighed by observers after finding the cache (n = 71), 2) Kestrel meal durations (n = 879), which were significantly correlated with the prey mass eaten (Fig. 1), 3) nest deliveries weighed during observations with weighing platforms in the nest-boxes (n = 239), and 4) voles collected in break-neck trap censuses in the study area (n =1100). During summer the mean mass of voles caught by Kestrels was smaller than that of voles trapped. During reproduction (April-July) males treated the voles caught selectively. The voles eaten immediately after capture had a smaller mean body mass than voles delivered to the dependents or voles cached. Voles delivered to the female and/or the nestlings had a smaller mean body mass than voles cached. During winter, the vole population was non-reproductive and homogeneous in size. Mean body mass of voles eaten or cached by Kestrels and of voles trapped were not distinguishable (Fig. 2, Table 2).

4. Water, fat, protein and ash contents of common voles analysed varied with season (Table 4). The energy content per g dry matter did not show significant seasonal variations (21.4 ± se 0.1 kJ/g). The assimilation quotient for a common vole diet in summer was higher than in winter. These variations resulted in a metabolizable energy equivalent of 4.6 kJ/g fresh in winter and 4.2 kJ/g fresh in summer.

5. In the non-reproductive season metabolizable energy intake varied with time of day. Intake rate increased at the end of the active day. In contrast energy intake in the reproductive season was constant over the active period.

6. Daily metabolizable energy intake in winter showed large day-to-day variations, related to weather conditions since there are severe meteorological constraints on flight-hunting (Fig. 4). Caching and retrieving prey buffers such variations.

7. Mean daily metabolizable energy intake varied through the annual cycle (Fig. 5, Table 6). In females the mean intake rate was highest during egg-laying (371.2 ± se 32.1 kJ/day), an elevation of 35% above the winter level. The mean intake rate of the males reached a maximum in the nestling phase (415.6 ± 42.3 kJ/day) an elevation of 52% above the winter level, and coinciding with the seasonal maximum in flight-activity . The minimum levels of intake and flight-activity (males and females during moult) also coincided. There was a correlation between daily energy intake rate and daily flight-hours, for male Kestrels tending nestlings (Fig. 6). On days with less flight-activity than average (4.6 h/day) male Kestrels seemed able to maintain a balance between energy intake and energy expenditure. On days with more than 4.6 flight-hours, the energy intake leveled off at a mean of 430.0 ± se 23.4 kJ/day. It is suggested that M in the latter condition was constrained by a limit to the total amount of food processed per day, which was insufficient to cover the energy costs.

8. The implications for the energy budget of seasonal variations in energy intake and time allocation are discussed. The Kestrel appears to use various options to meet seasonal peak energy demands: increased daily metabolizable energy intake, accumulation and mobilization of body reserves and changes in energy allocation to thermoregulation and activity.

6. ACKNOWLEDGMENTS

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8. SAMENVATTING

1. Natuurlijke seizoensvariaties in de dagelijkse opname van metaboliseerbare energie werden vastgesteld op basis van 375 waarneemdagen aan individuele Torenvalken. Prooisoort, aantal en duur van de maaltijden werden aan de gedragsprotocollen ontleend, energieinhoud en assimilatiequotient werden in het laboratorium bepaald.
2. Van oktober tot maart bestond het dieet voor 95% uit veldmuizen en voor 2% uit bosspitsmuizen. Van april tot september werden de veldmuizen in het dieet aangevuld met 6% bosspitsmuizen, 2% zangvogels en 1% steltloperjongen.
3. Veldmuisgewichten werden ontleend aan vier steekproeven: a) door Torenvalken verstopte muizen (n = 71); b) waargenomen maaltijdduur van etende valken (n = 879); c) door valken op van weegschalen voorziene nesten aangevoerde prooien (n = 239); d) veldmuizen gevangen bij twee-maandelijkse dichtheidsbepalingen met klapvallen (n = 1100). In de zomer waren de door valken gevangen muizen gemiddeld lichter dan de muizen in klapvallen. Tijdens de voortplanting behandelden mannelijke Torenvalken de geslagen veldmuizen selectief: Direct opgegeten muizen waren significant lichter dan de op het nest aangevoerde muizen, die zelf weer lichter waren dan verstopte muizen. De winterpopulatie veldmuizen vertoonde weinig variatie in gewicht en selectie werd dan ook niet vastgesteld.
4. Water-, vet-, eiwit-, en asgehaltes van veldmuizen varieerden in de loop van het jaar (Tabel 4), de energieinhoud bleef echter constant (21.4 ± 0.1 kJ/g). Door variatie in het assimilatiequotient waren er verschillen in de metabolische energiewaarde (zomer 4.6 kJ/g verse muis;winter 4.2 kJ/g).
5. Buiten het voortplantingsseizoen varieerde de energieopname over de dag, zodanig dat deze een piek vertoonde rond zonsondergang.
6. In de winter traden grote dagelijkse verschillen op in de energieopname, die vooral door weersomstandigheden werden bepaald (Fig. 4). Het verstoppen en weer ophalen van gevangen prooien bufferde zulke dagelijkse variaties.
7. Voor ♀♀ Torenvalken bereikte de gemiddelde dagelijkse opname een maximale waarde gedurende de eileg (371.2 ± 32.1 kJ/dag), een verhoging van 35% boven het winter niveau. Voor ♂♂ lag het maximum in de nestjongenfase (415.6 ± 42.3 kJ/dag), 52% boven de winteropname. Minimale voedselopname viel samen met de rui, zowel voor ♀♀ als voor ♂♂. Bij ♂♂ die hun jongen verzorgden bestond er een samenhang tussen de dagelijkse inspanning en de voedselopname (Fig. 6): Op dagen met minder dan gemiddelde inspanning (4.6 uur vliegen/dag) bleven opname en verbruik van energie in balans. Op dagen met hogere inspanning bleef de energieopname ongewijzigd op een niveau van 430.0 ± 23.4 kJ/dag. Vermoedelijk werd de opname beperkt door een grens aan wat per dag aan voedsel verwerkt kan worden en moesten boven de gemiddelde inspanning lichaamsreserves worden aangesproken.
8. De Torenvalk blijkt verschillende manieren te gebruiken om seizoenspieken in energiebehoefte het hoofd te bieden: verhoogde dagelijkse opname, aanleg en verbruik van lichaamsreserves en wisselende allocatie van energie voor warmteregulatie en activiteit.